AN ABSTRACT OF THE THESIS OF

Steven Clark for the degree of Master of Science in Fisheries Science presented on March 22, 2013

Title: Breeding Site Selection by Coho Salmon (*Oncorhynchus kisutch*) in Relation to Large Wood Additions and Factors that Drive Reproductive Success

Abstract approved:

Jason B. Dunham

The fitness of female Pacific salmon (*Oncorhynchus* spp.) with respect to breeding behavior can be partitioned into at least four components: survival to reproduction, competition for breeding sites, success of egg incubation, and suitability of the local environment near breeding sites for early rearing of juveniles. Accordingly, breeding sites should exhibit predictable habitat features linked to these components. In this study, I evaluated the relative influences of habitat features linked to fitness components on selection of breeding sites by coho salmon (*Oncorhynchus kisutch*). I also evaluated associations between breeding site selection and additions of large wood, as the latter were introduced into the study system as a means of restoring habitat conditions to benefit coho salmon. I used a model selection approach to organize specific habitat features into groupings reflecting fitness components and influences of large wood. The relative likelihood of each of these models was then evaluated based on how coho salmon were observed to select breeding sites. Specific variables examined within these models included depth at the redd, width to depth ratio, stream network location, proximity to other redds, maximum depth, proximity to a pool tail, and the count of naturally occurring and artificially placed large wood. Results of this work suggest that female coho salmon most likely select breeding sites based on habitat features linked to all four hypothesized fitness components. Linkages between large wood and breeding site selection were less clear, likely due to mismatches between the scale at which availability was quantified relative to the geomorphic influences of wood, insufficient time for wood to have geomorphic influences on habitat, or the directionality in which geomorphic effects are currently manifested (i.e., upstream, downstream, or bi-directional influences). Future work focused on geomorphic processes in this system could reveal stronger linkages between instream wood and the habitat features that coho salmon select for breeding.

Breeding Site Selection by Coho Salmon (*Oncorhynchus kisutch*) in Relation to Large Wood Additions and Factors that Drive Reproductive Success

by

Steven Clark

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented March 22, 2013
Commencement June 2013

Master of Science thesis of Steven Clark presented on March 22, 2013.

APPROVED:

____

Major Professor, representing Fisheries Science

____

Head of the Department of Fisheries and Wildlife

____

Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

____

Steven Clark, Author

ACKNOWLEDGEMENTS

First, I would like to thank my advisor, Jason Dunham, for determinedly nudging me from my wading boots to a keyboard, where I have learned more than could possibly be said here. Jason’s patience, guidance, and encouragement were instrumental to my success in this project. I could not have had a better teacher.

I would also like to thank Rebecca Flitcroft and Dana Warren for helping with my study design, providing fantastic insight along the way, and for sharing their wealth of knowledge. Their guidance was undoubtedly more helpful than I made evident.

Further, I would like to thank John Van Sickle for his statistical advice during study design and analysis phases of my project.

This project would not have been possible without the funding and support from the Bureau of Land Management and the United States Geological Survey- Forest and Rangeland Ecosystem Science Center. I am thankful for the many interactions I had with numerous individuals in these agencies. Specifically, it is an understatement to say this work would not have been possible without the overarching support and assistance of all kinds from Jeff McEnroe, Scott Lightcap, Daniel Dammann, Jacob Winn, and Sidney Post.

I would like to thank Ben Ramirez, Jared Blake, Rosie Gonzalez, Mike Heck, Doug Bateman, and David Leer for help collecting habitat data in Oregon’s Coast Range during all sorts of winter weather. These individuals helped keep spirits high, which led to a heaping amount of high quality data.

Knowledge, guidance, discussion, laughs, and more were vital components to my success as a graduate student, all of which were provided by the following lab mates, peers, buddies, and clubs: John Speece, Ben Ramirez, Rosie Gonzalez, Brooke Penaluna, Mike Heck, Maddie Eckmann, Ivan Arismendi, Mark Raggon, Emily Campbell, Matt Strickland, Kristen Kirkby, Rachel Reagan, Haley Ohms, Rachel Lovelford, Ryan Flaherty, David Hockman-Wert, Doug Bateman, David Leer, Levi Pienovi, the Coho Club, and Mondays @ 4.

I am so in debt to my wife, Hallie Clark, for her support and encouragement throughout my project. She sat through practice presentations and read through rough drafts that were meant for fish geeks and never blinked an eye. Hallie knew I would succeed even when I didn’t.

Last, but certainly not least, I want to thank my loved ones, The Clark, Focht, and Stratton Families, whose unwavering support and praise astounds me to this day.

TABLE OF CONTENTS

LIST OF FIGURES

Figure | Page

LIST OF TABLES

LIST OF APPENDIX TABLES

Breeding Site Selection by Coho Salmon (*Oncorhynchus kisutch*) in Relation to Large Wood Additions and Factors that Drive Reproductive Success

CHAPTER 1 – INTRODUCTION

Salmon are renowned for dramatic migrations from freshwater to sea, returning to reproduce in their natal streams (Groot and Margolis 1991; Quinn 1999). Whereas the complex life histories of salmon involve many challenges to growth and survival, the fitness of individuals that survive to reproduce is ultimately determined by their reproductive success, which may depend on sex-specific tactics (Fleming 1996). Among the factors that influence the fitness of females, breeding habitats linked to egg incubation and emergence have by far received the most attention (Bjornn and Reiser 1991; Sear and DeVries 2008). Although this is a key requirement, other conditions such as pre-breeding survival (Mann et al. 2010) and suitability of the local environment for early juvenile rearing (Einum et al. 2011) may also be important. In fact, all of these factors may play a role in determining locations that females select for reproduction (Cury 1994; Sear and DeVries 2008). In this study I evaluated selection of breeding sites (Hendry et al. 2001) relative to measurable habitat features related to the full range of factors that may drive fitness in breeding female salmon: the probability of survival to breeding, success of egg incubation and emergence, quality of juvenile rearing habitat, and competition among females for breeding sites. In addition to these factors I directly evaluated associations between breeding site selection and placement of large wood in the stream channel.

To evaluate selection of breeding sites by females in relation to habitat features, it is important to consider how reproductive success is linked to different stages of reproduction. The basic factors influencing reproductive success can be considered in a sequence of four stages: 1) adult survival, 2) competition among females for breeding sites, 3) egg incubation and survival of alevins, and 4) quality of habitat for rearing of recently emerged progeny. Reproduction is not possible for adults that do not survive through nest construction, oviposition, and covering phases of breeding, and it is reasonable to predict that breeding sites should be linked to instream features such as cover that can reduce the susceptibility of adults to predation (Hendry and Berg 1999; Hendry et al. 2001). Such habitats that promote survival during redd (nest) construction may be limited in their availability, sometimes leading to intense competition among females for breeding sites (Van den Berghe and Gross 1989; Fleming and Gross 1994). Of the local habitat features that influence breeding site aggregations, the suitability of the breeding site for egg incubation and survival of recently emerged alevins in stream substrates could be important (Chapman 1988; Jensen et al. 2009). Substrate conditions for incubation of eggs and alevins are likely factors influencing fitness. The redd environment is critical because salmon do not exhibit parental care (Esteve 2005). In semelparous species, selection of a poor breeding site may result in complete loss of female's contribution to the next generation (Hendry and Stearns 2003). Finally, breeding sites may be linked to survival of early rearing juveniles because dispersal shortly after emergence is generally limited, and thus features of habitat in the immediate vicinity of redds may drive juvenile survival (Beal et al. 1994; Teichert et al. 2011). In practice, evaluating the relative importance of these four factors in the field depends on how strongly they are related to measurable habitat features.

A broad range of habitat features may be related to the factors that drive selection of breeding sites, namely survival of reproducing adults, eggs and emerging alevins, and early rearing fry. The observation that salmon often select breeding sites adjacent to habitat features that can be used as cover such as depth and large wood (Bjornn and Reiser 1991; Merz 2001), suggests that cover plays an important role in survival of adults during reproduction. Whereas availability of cover for reproducing adults could be important, competition among females could limit availability of potential sites for breeding when local densities are relatively high (Hendry and Stearns 2003). If such is the case, redds may be spaced further apart than expected based on availability of suitable breeding sites, due to territorial defense by females. Alternatively, redds may be closer together than expected by chance if suitable habitat conditions are spatially clustered, and territorial defense has little influence on breeding site selection. Because the survival of eggs and emerging alevins is another critical component of a female's fitness, it stands to reason that females should select breeding sites located near transition zones between pools and riffles made up primarily of gravel substrate containing a small proportion of fine sediment (Bjornn and Reiser 1991; Kondolf and Wolman 1993; Kondolf 2000; Mull and Wilzbach 2007). Such transition zones are thought to offer quality incubation and emergence conditions because intergravel flow at these locations reduces the risk of embryo entombment, disease, and suffocation (Chapman 1988; Kondolf and Wolman 1993; Kondolf 2000). Stream features such as low velocity lateral habitat (Moore and Gregory 1988) and cover including large wood and depth (Nickelson et al. 1993; Allouche 2001) are thought to be important for the survival of newly emerged fry and should therefore generally be expected wherever breeding sites are located. Ultimately, the location of breeding sites selected by female salmon is potentially determined by all of these habitat factors, the degree to which they truly reflect processes that could influence females and the relative importance of each to the fitness of individuals.

Many habitat features known to influence selection of breeding sites such as presence of transition zones between pools and riffles, heterogeneity of depth and velocity as well as the accumulation of large wood are themselves influenced by the presence of large wood in stream channels (Keller and Swanson 1979; Crispin et al. 1993; Bilby and Bisson 1998; Gurnell et al. 2002). This is evident from studies showing that instream large wood can increase the size and frequency of pools, increase available sediment for reproduction, and increase availability of slow-water flow refuges (Keller and Swanson 1979; Crispin et al. 1993; Montgomery et al. 1995). Whereas large wood is responsible for creating many of the habitat features outlined here, the role of large wood to selection of breeding sites may be further influenced by habitat features that may not be easily described by measures proposed herein. Thus, it is reasonable to consider a direct association between breeding site selection and large wood, in addition to specific habitat factors.

The large body of literature demonstrating the geomorphic influences of large wood to stream habitats has motivated literally hundreds of local efforts to restore instream habitat for salmon, particularly in the Pacific Northwest USA (Katz et al. 2007). In this region, abundance of large wood in stream channels was dramatically reduced by past land use practices and active removal of wood (Sedell and Luchessa 1981; Sedell and Duval 1985; Lichatowich 1999; Stewart et al. 2009). Given this legacy of the loss of large wood in streams, actively restoring wood in streams would seem to be a sensible restoration action. This practice has been brought into question, however, because the evidence demonstrating the restorative value of these well-intentioned, but extensive and expensive efforts to salmon is debatable (Burnett et al. 2008; Stewart et al. 2009; Whiteway et al. 2010). To date, effectiveness monitoring with respect to large wood addition projects has focused on juvenile salmon abundance and survival, with a notable lack of information regarding breeding habitat use: a prerequisite for understanding how subsequent life stages are impacted (Groot and Margolis 1991). This distinction is critical because habitat that is beneficial for one life stage may not necessarily benefit others (Schluter et al. 1991; White and Rahel 2008). Whereas the physical function of large wood addition to streams is well studied, knowledge regarding potential effects to salmon reproduction is lacking.

For this study, I developed three objectives designed to explain the relative influence of a number of habitat features to selection of breeding sites by coho salmon (*Oncorhynchus kisutch*) in a western Oregon stream. The first was to spatially reference coho salmon redds in the study area. Second, I quantified features of habitat at sites used by breeding coho salmon as well as random locations that were available for use. Lastly, I used a resource selection function to estimate the relative probability of breeding site use in relation to measures of habitat linked to factors hypothesized to influence selection of breeding sites such as survival of adults during reproduction, competition between females for breeding sites, a redd environment that promotes successful incubation of eggs and emergence of alevins, quality of habitat for early rearing progeny, and the local abundance of natural and restored large wood. Given the overall lack of knowledge regarding the potential effects of large wood to salmon reproduction as well as the effect of habitat features specifically to selection of breeding sites, the implications of this study to stream management are relevant for understanding the basic needs of salmon during reproduction and effects of instream restoration using large wood.

CHAPTER 2 - METHODS

Approach

I adopted a resource selection approach to examine the influence of habitat features on selection of individual breeding sites by coho salmon (Manly et al. 2002). I employed a design where instances of use are known (e.g., redd sites), and availability is measured at random sites (potentially suitable, but unused) within the study extent (design II; Manly et al. 2002). Essential to resource selection functions are four key considerations. First, the appropriate variables driving site selection must be considered (Manly et al. 2002). Second, to correctly quantify habitat use, false identification of redds should be minimized and detectability of redds should be high (Dunham et al. 2001). Third, it is imperative to accurately determine the appropriate scale needed to quantify features of used and available habitat locations (Neville et al. 2006). Lastly, reasonable approximation of "availability" is necessary. With these general considerations in mind, I designed a sampling and analytical approach to evaluate breeding site selection by coho salmon.

Study Area

This study was conducted in Little Wolf Creek (area =23.75 km^2), a tributary of Wolf Creek in the Umpqua River basin, Oregon (Figure 1). Land ownership of the stream and riparian area is primarily Bureau of Land Management (BLM), whereas ownership upslope is a mosaic of BLM and private industrial forest. Climate in the Little Wolf Creek basin is characterized by wet winters, dry summers, and relatively mild temperatures (Chang and Jones 2010). Common riparian trees and shrubs include big leaf maple (*Acer macrophyllum*), red alder (*Alnus rubra*), salmonberry (*Rubus spectabilis*), Oregon myrtle (*Umbellularia californica)*, Douglas fir (*Pseudotsuga menziesii*), western red cedar (*Thuja plicata*), and western sword fern (*Polystichum munitum*). In addition to coho salmon, salmonids present include resident and andromous rainbow trout (*Oncorhynchus mykiss*), and coastal cutthroat trout (*Oncorhynchus clarkii clarkii*). Based on BLM surveys from 2006-2011, the average annual breeding distribution of coho salmon in Little Wolf Creek totals approximately 13.7 linear kilometers (J. McEnroe and S. Lightcap personal communication, Roseburg District Bureau of Land Management 2011; Figure 1).

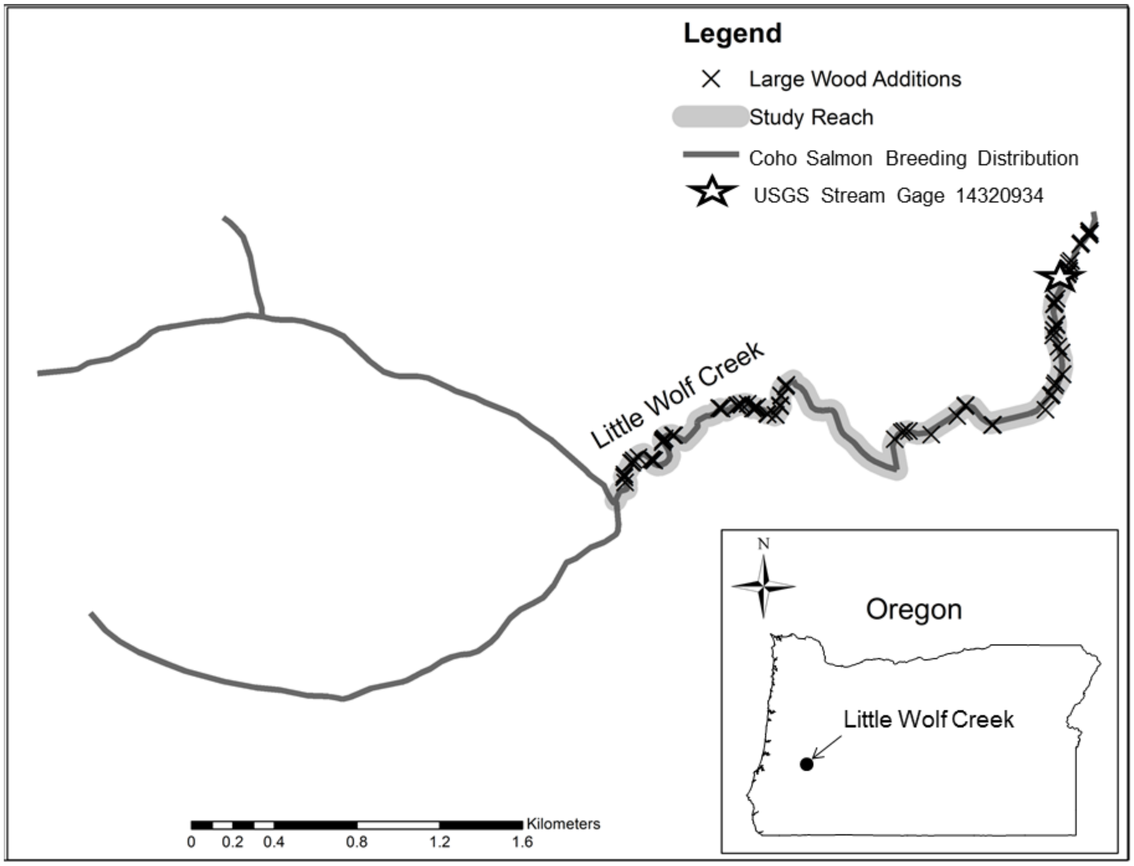

Figure 1. Map of Little Wolf Creek, Douglas County, Oregon. The map shows the studied reach, large wood additions, location of the U.S. Geological Survey stream gage 14320934, and the average annual breeding distribution of coho salmon based on surveys from 2006-2011 (J. McEnroe and S. Lightcap personal communication, Roseburg District Bureau of Land Management 2011).

Historical land use in Little Wolf Creek has not been thoroughly documented, but, physical evidence and limited records available suggest that stream cleaning and/or splash damming occurred in approximately the lower 30% of the stream (Sedell and Luchessa 1981; J. McEnroe and S. Lightcap personal communication, Roseburg District Bureau of Land Management 2011). To replace large wood lost in Little Wolf Creek through these practices, in 2008 and 2009 the BLM added 281 pieces of large wood to Little Wolf Creek, grouped into 37 channel spanning engineered log jams (ELJs). The primary objective of the log additions was to enhance the quantity and quality of breeding and rearing habitat for coho salmon. Accordingly, ELJs were constructed in stream locations that were perceived to most likely meet the restoration objectives. Features common to restoration sites prior to ELJ placement included low gradient (0.89%) lacking habitat features believed to be important for salmonids, including simplified channel form and lack of gravel or larger-sized substrates. ELJs were constructed with an average of six Douglas fir logs averaging 8.4m in length and approximately 76cm in diameter at breast height stream (J. McEnroe and S. Lightcap personal communication, Roseburg District Bureau of Land Management 2011), and were commonly pinned between two live trees to prevent downstream displacement whilst allowing them to interact in a semi-natural manner with the channel by rising and falling with varying discharge.

Study Design

Used Habitat

To assess breeding site selection by coho salmon relative to ELJs, I sampled a 4.5 kilometer subset of the total breeding distribution of coho salmon in Little Wolf Creek where ELJs were present (Figure 1). Within this study reach, all coho salmon redds (n=91) were examined during the 2011-2012 breeding season (November 17, 2011-February 14, 2012).

I quantified redd locations (= used breeding sites) by using a previously implemented linear spatial referencing system made up of sequentially numbered tree tags which were placed at known locations throughout the study reach. Redd sites were in the form of measured instream distances from tree tags to the center of the tailspill (Figure 2) of the nearest redd, which meant that the relative location of individual redds could be compared to each other. During the study period, the entire study reach was surveyed at least every 4 days to account for the possibility of redd features being obscured during periods of high flow as well as superimposition (i.e. overlap of two or more redds) which could lead to an inaccurate evaluation of used habitat. In an effort to reduce the likelihood of "double counting" a redd, each newly observed redd was marked with flagging and hung as close as possible to its tailspill (Figure 2). To reduce the possibility of including incomplete redds also known as "test redds" in any of my analyses, only redds in which a defined pit and tailspill was present were recorded as used habitat (Dunham et al. 2001). This is an important distinction since test redds are generally thought to be incomplete redds, and may subsequently designate the location of relatively poor breeding habitat (Crisp and Carling 1989).

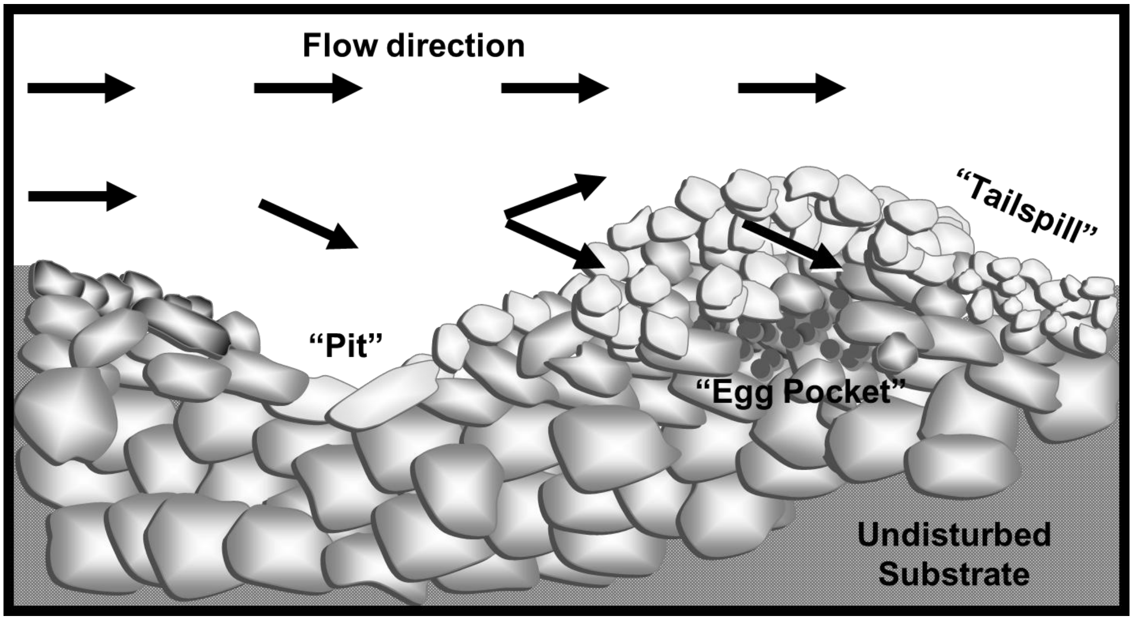

Figure 2: Features of a coho salmon redd (adapted from Dunham et al. 2009). Primary features of a redd include the pit, egg pocket, and tailspill. Female coho salmon actively remove smaller substrate particles from the stream bottom, typically forming an oval shaped depression in the substrate called a pit. Once the pit is excavated, oviposition and egg fertilization occur. Females fan gravel over the eggs (i.e. egg pocket) to cover them, and a tailspill or area of finer sediment is formed adjacent and downstream of the egg pocket. Water is forced through the egg pocket due to the increased hydraulic gradient associated with the general morphology of a redd (Burner 1951; Esteve 2005).

I measured a set of habitat features that I hypothesized would accurately describe use of breeding sites by coho salmon. These features included: linear location in the stream (i.e. distance from stream mouth), bankfull depth at the tailspill, a ratio of bankfull width/bankfull depth at the tailspill, closest distance to another redd, count of naturally occurring large wood, count of large wood pieces in an ELJ, maximum depth, and distance to the nearest pool tail. All features were measured to the nearest centimeter.

Linear stream location of used and available locations was considered to account for longitudinal gradients in environmental conditions that could lead to spatially autocorrelated patterns of habitat selection (Isaak et al. 2007; Flitcroft et al. 2012). I considered bankfull depth at the tailspill of a redd to provide a consistent and flow-independent frame of reference to indicate habitat that could be used as cover during reproduction. The ratio of bankfull width/bankfull depth was examined because use of breeding sites may be linked to the presence of rearing habitat for newly emerged fry. Accordingly, I hypothesized that the probability of breeding site use would be greatest when bankfull width/bankfull depth is relatively high (i.e. relatively broad and shallow channel) because it may signify off channel habitat suitable for overwintering of juveniles (Nickelson et al. 1993; Solazzi et al. 2000) as well as low velocity margin habitat for fry in spring and summer (Moore and Gregory 1988). The closest distance to another redd was measured within the study reach because a spatial relationship may exist between redds in that at finer scales redds could be relatively evenly distributed due to competition between females, whereas at larger scales the distribution of redds may be relatively clumped where suitable habitat is present.

I counted the number of large wood pieces (≥ 15cm in diameter and 3m in length) in an ELJ as well as surrounding naturally occurring large wood of the same size because breeding site use could be influenced by the size of the large wood accumulation (i.e. larger accumulations should have a greater geomorphic influence). Large accumulations of large wood could be used as cover by multiple life stages (Andrus 1988; Allouche 2002) or create cover such as deep pools through scour downstream of large wood (Gurnell et al. 2002). The maximum depth was examined because adults and juveniles can use depth itself as cover (Berg et al. 1998). Lastly, I considered distance to the nearest pool tail because salmonids often reproduce in such transitional areas where streambed morphology can force downwelling (Bjornn and Reiser 1991; Geist and Dauble 1998). Except for the habitat features linear stream location and closest distance to another redd which were spatially referenced wherever they occurred in the study extent, all other used and available habitat features were examined within the "activity area" (Compton et al. 2002) of a redd. I use the term activity area in reference to the area around a redd that is most likely used by female coho salmon following selection of a breeding site. This space has been previously described as an area formed by the territorial tendency of female coho salmon to prevent other females from breeding too close, resulting in an average inter-redd space of $12.8m^2$ (Burner 1951; Sear and DeVries 2008). Subsequently, I examined habitat use within the activity area of a redd- the 20m space up and downstream (total=40m) from the tailspill of a redd. I elected to survey habitat use at a larger scale than what Burner (1951) suggested, because I suspected that breeding sites should be distributed not only based on territorial constraints, but also on selection for habitat that is most likely to increase survival or fitness of breeding females.

Available Habitat

The same set of habitat features measured for used habitat were also recorded for available habitat (*n*=278). I located available habitat points using a randomly generated array of x-y coordinates (i.e., x=lateral location within the bankfull width, y = distance upstream from mouth) within systematically spaced 30m longitudinal increments throughout the study reach. This allowed a degree of randomness and representation of available conditions. In addition to such spatial considerations, the possibility of temporal bias to habitat measurements such as variability of discharge (water depth) during the study period was minimized by employing flow-independent measures of habitat conditions. Because coho salmon are unlikely to reproduce in locations without suitable substrate (Burner 1951; Reiser and Bjornn 1979; Kondolf and Wolman 1993), I considered locations with <30% of the substrate classified as gravel/pebble as unavailable. Similarly, since redds were never observed in locations with bankfull depths exceeding 1.5m, locations exceeding these depths were also excluded from the pool of available locations

Critical to use and availability studies is the assumption that available habitat is not used during the study period. However, this assumption is not always true (Manly et al. 2002). Habitat classified as available may actually be used, but not detected during sampling (Johnson et al. 2006). For example, the identifying features of a redd (Figure 2) may become obscured during periods of high flow, or use of habitat may depend on population density observed at the time of the study (e.g., Isaak et al. 2007). These issues pose challenges for estimating the absolute probability of use (Keating and Cherry 2002; Johnson et al. 2006), but the relative probability of use can nonetheless provide key insights (Compton et al. 2002; Manly et al. 2002).

Statistical Methods

I first compared used and available habitat features using non-parametric Wilcoxon rank-sum tests. Comparisons between used and available habitat were made for each explanatory variable considered in this study (Table 1). All statistical procedures were carried out using R version 2.15.1 and an alpha level of 0.05 was used for all statistical tests when frequentist inferences were applied.

I developed a set of candidate models (Burnham and Anderson 2002) based on factors hypothesized to influence selection of breeding sites by female coho salmon. The model categories were *cover*, *competition, incubation, progeny,* and *large wood*, each of which were made up of linear parameters that were linked through literature or hypotheses to selection of breeding sites by coho salmon (Table 1). The cover model was developed because habitat that can be used as cover could increase the probability of adult survival to reproduction. Accordingly, the parameters depth, naturally occurring large wood, ELJ, maximum depth were included in the cover model because they could all be used as cover by coho salmon during breeding. An incubation model was included because a quality incubation environment may increase survival of incubating eggs and the success of emerging alevins. The progeny model was considered because the survival of early rearing fry may translate to fitness benefits for breeding females. A competition model seemed plausible because competition may exist for breeding sites. Additionally, I was interested in the potential impact of ELJs and naturally occurring large wood to breeding site use, so a large wood model was constructed. Finally, a full model was developed that contained the complete set of habitat variables because breeding site use could be influenced by multiple factors that influence coho salmon survival (Table 1).

I used logistic regression to examine the relative probability of use of habitat features presumed to be used during breeding by comparing used and available habitat features (Hosmer and Lemeshow 2000; Ramsey and Schafer 2002). This analysis makes it possible to evaluate the relative roles of hypothesized processes (i.e., candidate models and parameters; Table 1) that potentially drive selection of breeding sites by coho salmon. For each candidate model I derived Akaike’s information criterion (AIC) corrected for small sample sizes to determine the relative plausibility of each candidate model (Burnham and Anderson 2002). The change in value, corrected for small sample size (AIC_c) between the highest ranking model and each other model was calculated and assigned to each model and model weights (AIC_w) were derived from these values.

Before comparing logistic models I checked the assumptions of spatial independence of residuals and absence of multicollinearity of predictors used in the logistic regression model. To check these assumptions, I calculated variance inflation factors to assess potential multicollinearity among variables included in all candidate models and the possibility of spatial autocorrelation was examined using a Mantel's test (Ramsey and Schafer 2002). To determine the predictive accuracy of the full model, a Receiver Operating Characteristic (ROC) curve was examined (Fielding and Bell 1997; Manel et al. 2001). An ROC curve is constructed by plotting the rate of true positives on the vertical axis and the rate of false positives on the horizontal axis for multiple thresholds. With this method a penalty for selecting an inadequate threshold is not needed because a full range of thresholds are used to construct the curve. A hypothetical area of one under the ROC curve (AUC) would represent a perfectly predictive model.

The influence of habitat variables on selection of breeding sites was determined by estimating the relative odds of breeding site use. To aid biological interpretability regarding the influence of stream location to the odds of breeding site use, a scaled constant was used to calculate the odds of breeding site use. For example, the coefficient for location was multiplied by 500 meters, which were judged to be more biologically meaningful than one meter units of measure. The relative odds of breeding site use were calculated using this scaled coefficient, where only the scaling of the odds ratio is changed (Hosmer and Lemeshow 2000).

Table 1. Habitat features grouped into models and hypothesized influences on breeding site selection by female coho salmon. Model names correspond to major components contributing to the fitness of females, or influences of large wood. Shown are candidate models and groupings of parameters for each. As the value of a variable increases, the probability of breeding site use is hypothesized to increase (+), decrease (-), or have a non-linear relationship (+,-; signifying a convex non-linear relationship). Note than non-linear terms were not included in this analysis.

Candidate Model	Stream Location	Depth	Width/ Depth	Closest Redd	Natural Wood	ELJ	Max Depth	Dist. to pool tail
Full	+	+,-	+	+,-	+	+	+	-
Cover		+,-			+	+	+	
Incubation								-
Progeny			+		+	+	+	-
Competition				+,-				
Large Wood	+				+	+		

CHAPTER 3 - RESULTS

The first and last coho salmon redds of the 2011-2012 breeding season were detected in the study reach on November 29, 2011 and January 31, 2012 respectively. During this period 91 redds were detected, only six of which were classified as superimposed. Initial construction of redds at breeding sites (resolution ≤ 4 days) consistently occurred near maximum discharges during the study period (Figure 3). Discharge during the study period ranged from 0.9 to 194.8 $m^{3}\cdot s^{-1}$ with a median of 3.7 $m^{3}\cdot s^{-1}$, and water temperature ranged from 1.9 to 9.3° C with a mean of 5.7° C.

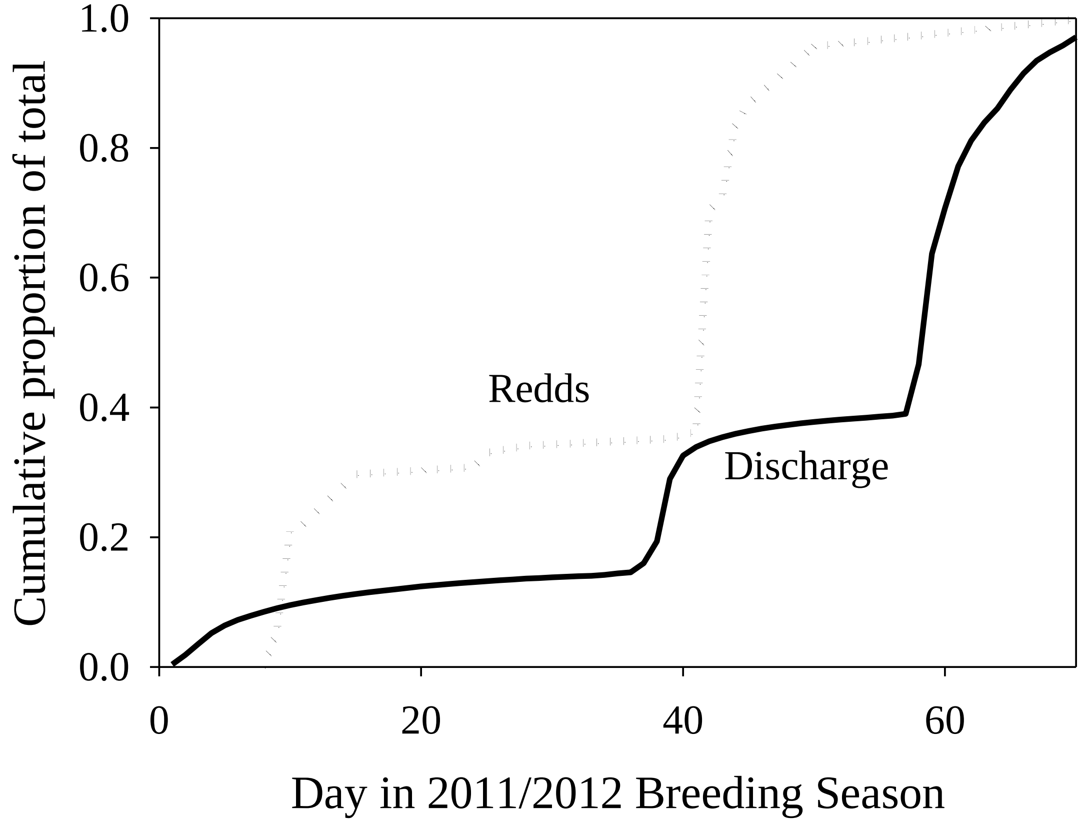

Figure 3. Cumulative proportion of redds vs average daily discharge during the 2011/2012 breeding season (November 17, 2011- February 14, 2012). The solid line represents average daily stream discharge ($m^3 \cdot s^{-1}$) and the dotted line represents the cumulative proportion of redds.

Significant differences between used and available locations occurred for four of eight habitat parameters (Table 2). The location relative to the stream mouth and the ratio of width to depth at the sampling point for used sites were not significantly different than that for available sites. Depth at the sampling point was deeper ($W = 16066$, $p<0.001$) for used than available sites and the maximum depth within the activity area (+/- 20m) was greater ($W = 21251$, $p < 0.001$) for used than available sites. The distance from used sites to a redd was significantly shorter than for available sites ($W = 8986$, $p <0.001$). The number of large wood pieces in ELJs or pieces that were naturally occurring within the activity area was not different for used and available sites. Sites used by coho salmon were closer to pool tails than those that were available ($W = 7875$, $p <0.001$).

Table 2. Used and available means and standard deviations for all parameters in the full model. An asterisk "*" represents a statistically significant difference in medians as examined by a Wilcoxon rank-sum test (α <0.05).

	Used		Available
Location	3006.24 +/- 1068.25		2815.98 +/- 1234.16
Depth	0.93 +/- 0.18	*	0.84 +/- 0.17
Width/Depth	16.25 +/- 5.08		16.13 +/- 5.65
Closest Redd	16.68 +/- 36.51	*	28.12 +/- 40.60
ELJ	4.07 +/- 6.89		3.97 +/- 6.79
Natural Large Wood	6.07 +/- 5.88		6.94 +/- 8.35
Max Depth	1.61 +/- 0.17	*	1.38 +/- 0.21
Distance to Pool Tail	5.04 +/- 4.35	*	7.94 +/- 5.07

Model selection indicated the full model with the variables; location, depth, width/depth, closest redd, ELJ, natural large wood, maximum depth, and distance to the nearest pool tail (Table 1) was by far the most likely, given patterns of breeding site use by coho salmon (Table 3). The relative Akaike weight (AIC_w) of the full model was 0.999 indicating a 99.9% chance that it was the best approximating model given the set of candidate models considered here.

Table 3. Six candidate models developed according to factors that were hypothesized to influence breeding site selection by female coho salmon (Table 1). Corresponding degrees of freedom, corrected Akaike scores (AIC_c), changes in score from the “best” ranked model of the set (ΔAIC_c) and weight (AIC_w)are listed for each model.

Model	*Df*	AIC_c	ΔAIC_c	AIC_w
Full	9	292.85	0	0.999
Cover	5	322.91	30.06	<0.001
Incubation	2	390.63	97.77	<0.001
Progeny	6	316.46	23.61	<0.001
Competition	2	409.20	116.34	<0.001
Large Wood	4	417.82	124.97	<0.001

Given the overwhelmingly high rank of the full model relative to the set of candidate models (Table 3), data analysis from this point forward was conducted solely on the full model. Variance inflation factor indexes were less than ten for all parameters in the full model, thus there was little to no concern for multicollinearity. A Mantel's test comparing distance matrices of linear instream locations and residuals from the full model suggested that there was no significant evidence of spatial autocorrelation in the full model (*p*-value= 0.62).

A visual check of the accuracy of the full model using a receiver operator characteristic (ROC) curve suggested the model sufficiently predicted breeding site use by coho salmon in Little Wolf Creek (Figure 4). This was supported by a statistical assessment of the accuracy of the full model which yielded an AUC of 0.73, considered to be adequately accurate (Swets 1988).

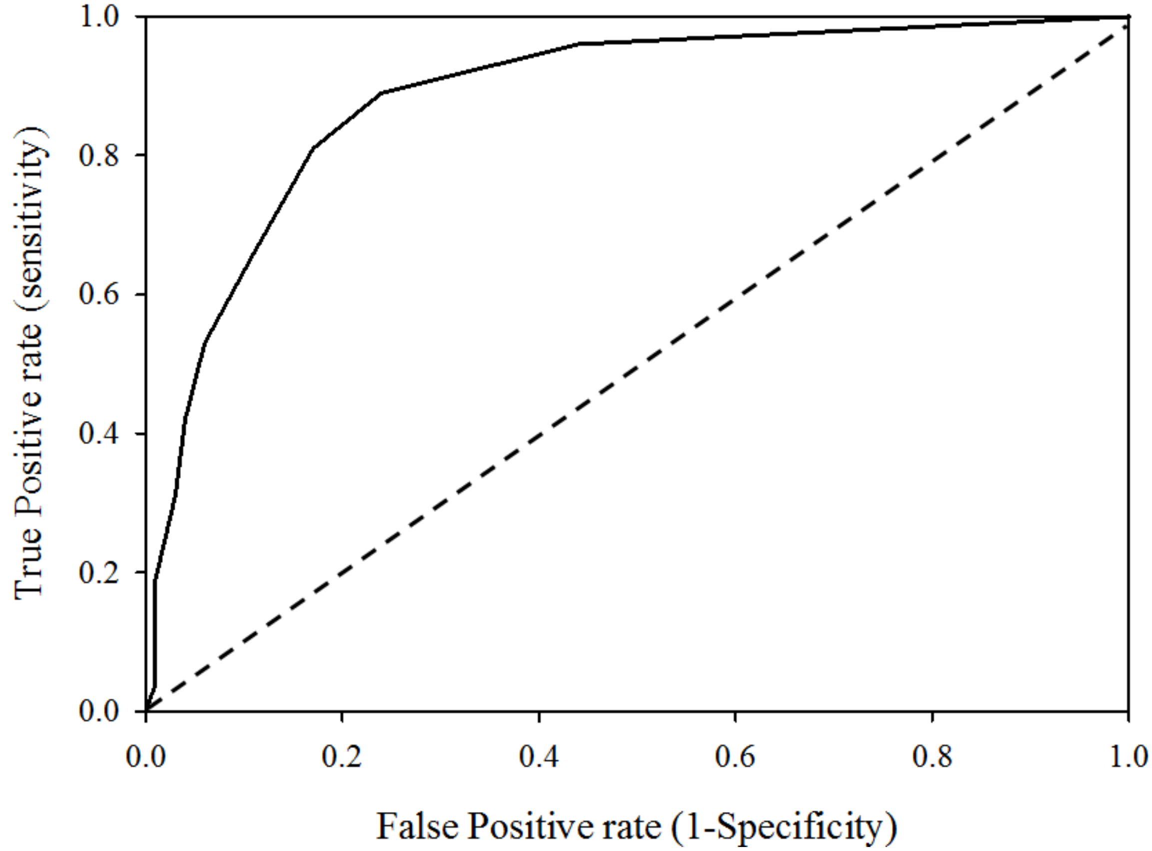

Figure 4. A ROC curve for the full model. The 45 degree dashed line represents a visual reference of a lower bound (i.e. poor performance) for a ROC curve.

Output from the logistic regression on the full model (Table 4) was transformed to odds ratios (Hosmer and Lemeshow 2000; Ramsey and Schafer 2002) to aid in the biological interpretation of parameter estimates (Figure 5; Table A.1). As expected (e.g., Table 2), three factors, depth at the sampling point, maximum depth within the activity area, and distance to a pool tail, were most influential. An increase in depth (to the observed upper limit of 1.5m) of 10 cm at the sampling point resulted in a 57% increase in the probability of a site being used. An increase in the maximum depth of 10 cm resulted in a 94% increase in the probability of a site being used. When the remaining parameters are held fixed the odds of breeding site use decreased by 14% as the distance *away* from a pool tail increased by 1m.

Table 4. Parameter estimates of the logistic regression on the full model for predicting breeding site selection by coho salmon.

Parameter	Estimate	S.E.	z value	*p*-value
Intercept	-15.22	2.13	-7.14	<0.001
Location	0.0003	0.001	2.17	0.029
Depth	4.53	1.20	3.76	<0.001
Width/depth	0.07	0.04	1.98	0.047
Closest Redd	-0.01	0.005	-2.51	0.012
ELJ	-0.05	0.02	-2.22	0.026
Natural Wood	-0.05	0.03	-2.25	0.025
Max Depth	6.61	0.9	6.97	<0.001
Dist. to Pool Tail	-0.20	0.03	-4.29	<0.001

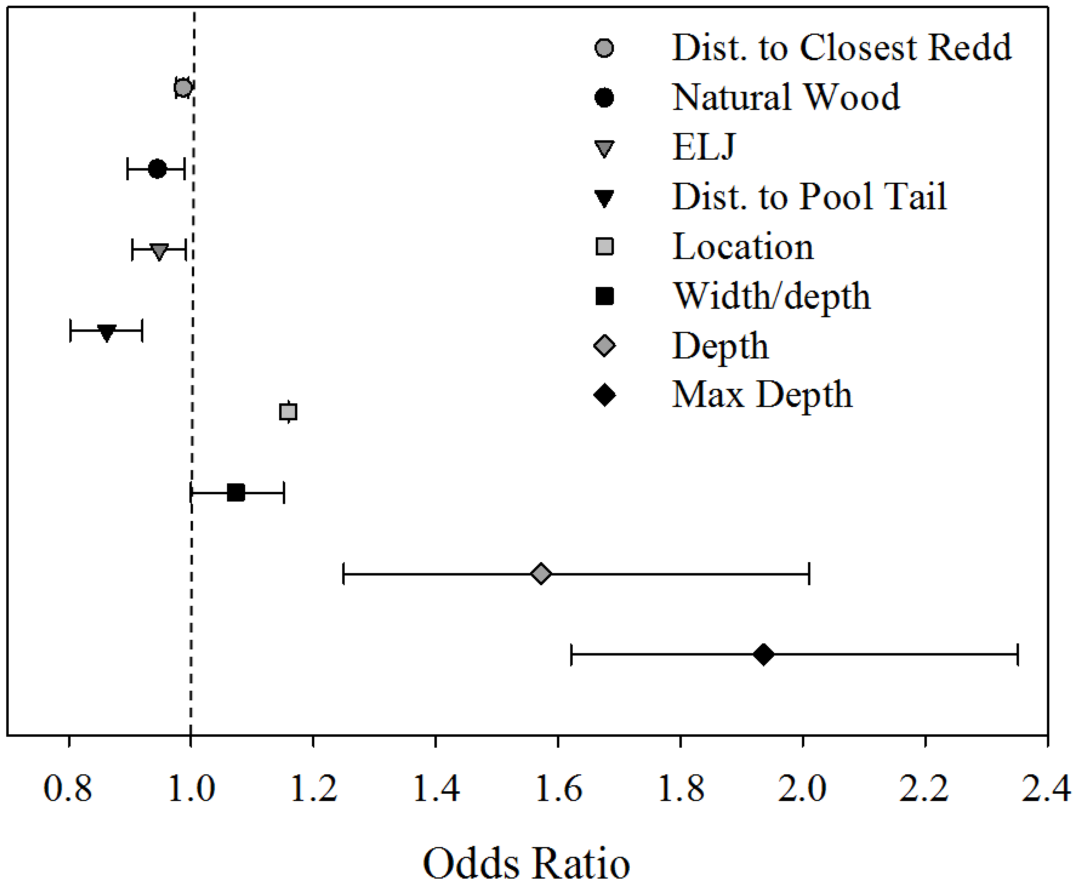

Figure 5. The relative odds of breeding site use given the parameters in the full model. Odds ratios <1 generally correspond to a decrease in the odds of breeding site use, whereas those >1 correspond to an increase in the odds of breeding site use. Note that the coefficient of location was scaled by a constant of 500m to increase its biological interpretability (see text narrative for detail).

CHAPTER 4 - DISCUSSION

This study is only one of two such efforts I am aware of (see also Mull and Wilzbach 2007) to evaluate breeding site selection by coho salmon, despite the fact the species is currently listed as threatened over much of its range in the Pacific Northwest (Good et al. 2005). Recent reviews of breeding habitat for salmonids have focused more on habitat itself (Sear and DeVries 2008) and less on the process of habitat selection. Conversely, recent reviews of evolutionary adaptations of salmonids have not considered habitat (e.g., Hendry and Stearns 2004). Habitat selection is critical to understand because it presumably represents a behavioral adaptation that is assumed to increase individual fitness (Cury 1994). Results of this work suggest that female coho salmon select breeding sites based on a wide range of habitat features linked to pre-breeding survival, competition for breeding sites, egg incubation, and suitability of local habitats for recently emerged juveniles. Understanding these habitat linkages is critical for protection and restoration of habitat conditions to support coho salmon. In this study I was unable, however, to identify a direct linkage between selection of breeding sites and instream restoration, at least as related to the presence of engineered log jams intended to provide suitable habitat for coho salmon. The implications of these findings are discussed below, but first it is useful to evaluate the value of my overall approach in quantifying habitat requirements for breeding female coho salmon using resource selection functions.

This study applied a resource selection approach, which is founded on the evolutionary assumption that habitat selection is a behavior that increases individual fitness (Manly et al. 2002; Layland et al. 2011). Although this would seem to be a natural foundation for understanding breeding behavior of salmon (Cury 1994; McClure et al. 2008), the bulk of research regarding reproductive requirements of salmon is dominated by studies of habitat use or physical habitat features (Bjornn and Reiser 1991; Kondolf and Wolman 1993; Sear and DeVries 2008). In addition to a foundation of hypotheses linked to the ultimate drivers of resource selection (Table 1), application of a resource selection approach requires three key steps: accurate quantification of habitat use (i.e., redds in this study), delineation of availability, and the application of an index of selection or statistical model to predict probability of use relative to availability (Manly et al. 2002). Following through on these steps can involve several challenges, of which the first two are considered in more detail here (for reviews of modeling approaches see Keating and Cherry 2004; Thomas and Taylor 2006).

Quantification of use can be an imperfect process, with attendant influences to reliability of parameters estimated with resource selection functions (MacKenzie 2006). In the case of redd counts, it is possible to commit errors of omission (failure to detect a redd that is present), as well as commission (classifying features as redds that are not bona-fide redds; Dunham et al. 2001). Such errors can lead to substantial problems with resource selection functions if probabilities of detection (including errors of omission and commission) cannot be accounted for (MacKenzie 2006). In this study, redds were closely tracked to eliminate, or at least to minimize these errors (Dunham et al. 2009). Determination of availability also poses problems in resource selection studies. To delineate availability accurately, it is essential that habitat availability is likely to translate to suitability for an organism. Suitability is important because a site could be un-used, but may not sufficiently satisfy a basic habitat requirement. For example, in this study I limited inferences about selection of breeding sites to locations with enough gravel of suitable dimensions to support breeding use (Kondolf and Wolman 1993; Sear and DeVries 2008). With regard to breeding site selection this feature was deemed to be absolutely necessary, whereas other factors may not exert such absolute control on habitat suitability.

A second consideration in determining availability is the spatial grain or resolution at which individuals perceive and select habitat (Compton et al. 2002; Boyce 2006; Thomas and Taylor 2006). In fact, different habitat features may be selected at different scales. For example, local channel morphology (e.g., within a meter or two) may drive bed forms and grain sizes of sediment that females select for egg incubation, whereas habitat features used for cover (e.g., depth, wood) may be more broadly distributed (e.g., over a 20m activity area). In contrast, proximity to the next closest redd was measured within the extent of the study reach because competition for space could occur across a longer distance (>20 m). These choices, founded herein on hypothesized behaviors that coho salmon exhibit during breeding, could strongly influence interpretation of breeding site selection.

Finally, the density of individuals within a given location can influence habitat selection (Morris 1989; Morris et al. 2000). When population densities are high, most highly suitable breeding site locations may be used, limiting their availability and possibly leading some females to be less selective. For example, selection of breeding locations by Chinook salmon (*O. tshawytscha*) in a stream network varied with local population density (Isaak et al. 2007). During years of lower densities, Chinook salmon redds were located only within larger and presumably more suitable patches of breeding conditions, whereas in years with higher densities, redds were more widely distributed. Densities of reproducing adults the year this study was conducted were high relative to escapement during the previous five years (Table A.2), potentially leading females to be less selective. Evidence from this study suggests otherwise however, as the probability of a site being used for reproduction increased with proximity to another redd (Figure 5, Table A.1). This is the opposite of what I expected based on competition among females for access to limited availability of suitable breeding sites. This observation is, however, consistent with the possibility that suitable breeding conditions were either spatially clumped or that females were cuing in on one another in selecting breeding sites (Valone and Templeton 2002). Although it is difficult to precisely quantify the degree or even direction to which the density of breeding individuals influenced selection in this study, the possibility should be considered at least with respect to the interpretation of individual coefficients generally considered marginally statistically significant (e.g., $\alpha \sim 0.05$) because these relationships may be more likely to shift with varying density.

In this study, I hypothesized that fitness of reproducing females can be partitioned into four components (Schluter et al. 1991; Siepielski et al. 2011): survival of adults, competition among females for breeding site locations, egg incubation and survival of alevins, and quality of habitat for rearing of recently emerged progeny (Table 1). Accordingly, I developed candidate models reflecting each of these components, and applied model selection to determine which was the most plausible, given the data. Through this process, I found the full model, incorporating all fitness components, was by far the most likely, given the observed pattern of breeding site selection by coho salmon (Table 3). This suggests all of the factors considered may shape breeding site selection to varying degrees. In some cases, individuals can face tradeoffs when resource requirements for different components of fitness are not complementary but rather conflicting (Schluter et al. 1991; Siepielski et al. 2011). For example, the "egg-fry" conflict hypothesized for salmonids (Quinn 2004) refers to a situation whereby a suitably cold egg incubation environment may be too cold or unproductive to support optimal growth of juveniles. In such cases individuals must be able to locate complementary resources in two or more locations (e.g., Dunning et al. 1992). In this study, I did not find evidence in support of such conflicts for the four components of fitness and associated habitat variables used for analysis of breeding site selection. Perhaps the larger activity area over which I considered breeding site selection can explain why such conflicts were not evident. As discussed above, the grain of availability used to analyze habitat selection can influence the view of which factors are most important. In this case, the larger grain of my activity area (40m) may have captured all of the complementary factors that influence breeding site selection by females, whereas studies at a finer grain may be more likely to detect effects of variables linked to the incubation environment (Geist and Dauble 1998; Baxter and McPhail 1999; Kondolf 2000).

Although I found that breeding site selection by female coho salmon was tied to a broad suite of habitat variables, three in particular; distance to the nearest pool tail, depth at the tailspill, as well as maximum depth played a dominant role (Figure 5). This finding suggests that selection of breeding sites was largely driven by proximity to a pool tail or riffle crest and supports the conclusion of other studies that areas of high intergravel exchange increase quality of the hyporheic incubation environment for salmonids (Bjornn and Reiser 1991; Geist and Dauble 1998; Baxter and Hauer 2000). In the case of water depth, breeding sites were more likely to occur as depth at a potential redd location increased, and similarly, the probability of breeding site use increased as maximum depth increased within the hypothesized activity area for a female. The influence of these depth variables on breeding site selection could reflect the importance of predator refuge for survival during reproduction, but additional influences of depth should also be considered. For instance, increased pool depth generally equates to increased hydraulic gradient which induces downwelling at the tail of a pool (Kondolf 2000). Downwelling can increase the supply of dissolved oxygen and flush waste products, thus increasing the suitability of pool tails for egg incubation and survival of recently emerged alevins (Chapman 1988).

Habitat variables, such as stream location and width/depth ratio at the tailspill of redds were only weakly associated with selection of breeding sites (Figure 5). Part of the reason for why these variables were less important may be linked to the ability of recently emerged juveniles to disperse from redds to find more suitable rearing locations

(Solazzi et al. 2000; Kahler et al. 2001; Teichert et al. 2011). The relatively weak influence of distance upstream could be tied to a variety of factors, including the importance of localized movement versus homing as drivers of breeding site location (Cury 1994; Neville et al. 2006). Because most females reproduce upstream of areas I studied, I expected that upstream distance, or proximity to these locations, would strongly and positively influence the probability of breeding site selection. Although the probability of breeding site use did increase in an upstream direction, the influence was relatively weak. This suggests the possibility that females are not simply homing to natal locations to reproduce within the system I studied, but exhibit some degree of localized movement and selective behaviors (Cram et al. 2013). Alternatively, it is plausible that females select breeding sites based on habitat features tied to more immediate factors that influence fitness, such as pre-breeding survival, breeding, and incubation of eggs and alevins (Table 1). This could be the case, in spite of the fact that the full model was most statistically plausible relative to the alternatives considered here.

It is also noteworthy that the previously discussed variables influenced habitat selection, as predicted, but that naturally occurring large wood and ELJs were unexpectedly found to be negatively associated with the probability of breeding site use. This association, although relatively weak (Figure 5), was unexpected because large wood is often responsible for the formation of habitat features such as heterogeneity of depth and width as well as increased pool frequency (Keller and Swanson 1979; Crispin et al. 1993; Montgomery et al. 1995; Bilby and Bisson 1998; Gurnell et al. 2002). Based on past work, it was reasonable to have expected that the probability of breeding site selection would increase due to the presence of large wood because the habitat features that large wood is often responsible for forming such as increased maximum depths and proximity to a pool tail (i.e. increased pool frequency) were found to increase the probability of breeding site use (Figure 5).

There are at least three possible explanations for lack of an association between ELJs and breeding site selection observed here. The first explanation is the possibility that not enough time has surpassed since ELJ construction for the formation of habitat that female coho salmon require for reproduction. Habitat conditions selected by females, particularly availability of suitable breeding substrates (Mull and Wilzbach 2007) could take considerable time to form or accumulate especially where ELJs are constructed in degraded locations (Wallace et al. 1995; Hogan et al. 1998). The idea that relatively degraded locations could take longer to restore is important because ELJs in Little Wolf Creek were purposely constructed in areas that were highly degraded relative to other areas in the stream. The second explanation is that the process of habitat selection or the behavior of females during reproduction does not match the scale of geomorphic processes which create habitat that females require for reproduction. In other words, the area of stream that is geomorphically influenced by an ELJ is probably much greater than the area within an activity area (suggested from field observations), and thus it is possible based on the design of this study, that a female could select habitat that was geomorphically formed by an ELJ, but that the ELJ itself is not located within the activity area associated with that redd. In my field observations, I noticed that a continuum of substrate sizes should occur upstream and adjacent to ELJs within “the area of geomorphic influence” or the area inundated by dammed pools that form upstream of ELJs during relatively high flow (Keller and Swanson 1979; Gurnell et al. 1995; Hogan et al. 1998). Within this area of geomorphic influence, water velocity is generally lowest relatively close to an ELJ which equates to a continuum of increasing substrate sizes with increasing distance from an ELJ. Subsequently, because coho salmon select gravel diameter substrate for reproduction (Mull and Wilzbach 2007), suitable breeding sites within the “area of geomorphic influence” may actually be further from ELJs that create relatively large and low velocity dammed pools compared to those that create relatively small and high velocity dammed pools (Wallace et al. 1995; Hogan et al. 1998). A final explanation for lack of an association between breeding site use and ELJs is that only the area upstream of ELJs could be geomorphically influenced. This is because ELJs in Little Wolf Creek were constructed on bedrock and thus formation of the expected scour of sediment downstream of ELJs did not occur because there is no currently none available. If sediment was present, scour downstream of ELJs could form relatively deep plunge pools and deposit gravel in pool tails. Future delivery of sediment to the stream channel may ultimately produce very different outcomes for the quality of breeding habitats in this system.

A longer-term view of restoring habitat conditions with ELJs in Little Wolf Creek may be more appropriate, given the strong legacy of impacts in the system (J. McEnroe and S. Lightcap personal communication, Roseburg District Bureau of Land Management 2011). Degraded habitat conditions that were the result of direct removal or displacement of large wood decades prior to this study and the addition of large wood in Little Wolf Creek may take decades or longer to reverse. My field observations suggest that even naturally occurring large wood was not substantially interacting with the actively influenced portion of the stream, and thus could not form instream habitat that is generally expected wherever large wood is present (Keller and Swanson 1979; Gurnell et al. 1995). Further, because habitat in the study reach was highly degraded, it is reasonable to surmise that relatively newly recruited (naturally occurring) large wood and ELJs are acting similarly at this stage. Over time the benefits of ELJs may be realized more fully as they interact with episodic delivery of sediment and natural large wood to the stream, providing opportunities for channel reorganization and the return of habitat conditions that are more suitable for coho salmon (Reeves et al. 1995; Hogan et al. 1998).

CHAPTER 5 - CONCLUSION

The comparison of habitat used for reproduction to that which is available for use is useful approach for evaluating the influence of stream features to reproductive success of coho salmon, which is at least to some extent the product of multiple components that influence survival for several life stages. Survival of these life stages appears to be linked to selection of breeding sites, which is tied to stream habitat features. Such features are absent in some systems, therefore efforts to restore them can be vital for sustaining salmon. To maximize the effectiveness of restoration, site specific geologic and geomorphic conditions should be prerequisites to project implementation. Furthermore, the intended effects of restoration projects may take considerable time to manifest due to the legacy of past land use, and accordingly project evaluation should ideally be planned over longer (>10 yr) timeframes to capture the range of effects to biotic and abiotic responses.

BIBLIOGRAPHY

Allouche, S. 2001. Nature and functions of cover for riverine fish. Bull. Fr Peche Piscic 365: 297-324.

Andrus, C.W., Long, B.A., and Froehlich, H.A. 1988. Woody debris and its contribution to pool formation in a coastal stream 50 years after logging. Can. J. Fish. Aquat. Sci. 45: 2080-2086.

Baxter, J.S., and McPhail, J.D. 1999. The influence of redd site selection, groundwater upwelling, and over-winter incubation temperature on survival of bull trout (*Salvelinus confluentus*) from egg to alevin. Canadian Journal of Zoology. 77: 1233-1239.

Baxter, C.V., and Hauer, F.R. 2000. Geomorphology, hyporheic exchange and selection of spawning habitat by bull trout (*Salvelinus confluentus*). Can. J. Fish. Aqaut. Sci. 57: 1470-1481.

Beal, E., Dumas, J., Claireaux, D., Barriere, L., and Marty, C. 1994. Dispersal patterns and survival of Atlantic salmon (*Salmo salar L.*) juveniles in a nursery stream. ICES Journal of Marine Sciences 51 (1): 1-9.

Berg, N., Carlson, A., and Azuma, D. 1998. Function and dynamics of woody debris in stream reaches in the central Sierra Nevada, California. Can. J. Fish. Aqaut. Sci. 55: 1807-1820.

Bilby, R.E., and Bisson, P.A. 1998. Function and distribution of large woody debris. *In* River Ecology and Management. Edited by R.E. Bilby and P.A. Bisson. Springer-Verlag, New York, New York. pp. 324-341.

Bjornn, T.C., and Reiser, D.W. 1991. Habitat requirements of salmonids in streams. *In* Influences of forest and rangeland management on salmonid fishes and their habitats. *Edited by* W.R. Meehan. Am. Fish. Soc. Spec. Publ. No. 19. Bethesda, Maryland. pp. 83-138.

Boyce, M.S. 2006. Scale of resource selection functions. Diversity Distrib. 12: 269-276.

Burner, C. 1951. Characteristics of spawning nests of Columbia River salmon. Fisheries Bulletin 61: 97-110.

Burnett, K.M., Giannico, G.R., and Behan, J. 2008. A pilot test of systematic of systematic review techniques: evaluating whether wood placements in streams of the Pacific Northwest affect salmonid abundance, growth, survival or habitat complexity. Final report on findings, 4 February 2008. Oregon Department of Forestry, Salem, OR.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. New York, Springer.

Chang, H., Jones, J. 2010. Climate change and freshwater resources in Oregon. Oregon Climate Change Research Institute. Oregon Climate Assessment Report. *Edited by* K.D. Dello and P.W. Mote. College of Oceanic and Atmospheric Sciences, Oregon State University, Corvallis, Oregon. Pp 69-150.

Chapman, D.W. 1988. Critical review of variables used to define effects of fines in redds of large salmonids. Trans. Am. Fish. Soc. 117: 1-21.

Compton, B.W., Rhymer, J.M., and McCollough, M. 2002. Habitat selection by wood turtles (*Clemmys insculpta*): an application of paired logistic regression. Ecology 83: 833–843.

Cram, J.M., Torgersen, C.E., Klett, R.S., Pess, G.R., May, D., Persons, T.N., and Dittman, A.H. 2013. Tradeoffs between homing and habitat quality for spawning site selection by hatchery-origin Chinook salmon. Environ. Biol. Fish. 96: 109-122.

Crisp, D.T., and Carling, P.A. 1989. Observations on sitting, dimensions, and structure of salmonid redds. Journal of Fish Biology 34: 119–134.

Crispin, V., House, R., and Roberts, D. 1993. Changes in instream habitat, large woody debris, and salmon habitat after the restructuring of a coastal Oregon stream. North American Journal of Fisheries Management 13: 96-102.

Cury, P. 1994. Obstinate nature: an ecology of individuals. Thoughts on reproductive behavior and biodiversity. Can. J. Fish. Aquat. Sci. 51: 1664-1673.

Dunham, J.B., Rieman, B.E., and Davis, K. 2001. Sources and magnitude of sampling error in redd counts for bull trout. North American Journal of Fisheries Management 21: 343-352.

Dunham, J.B., Rosenberger, A.E., Thurow, R.F., Dolloff, C.A., and Howell, P.J. 2009. Coldwater fish in wadeable streams. *In* Standard methods for sampling North American freshwater fishes. *Edited by* S.A. Bonar, W.A. Hubert, and D.W. Willis. American Fisheries Society, Bethesda, Maryland. pp. 119-138.

Dunning, J.B., Danielson, B.J., and Pulliam, H.R. 1992. Ecological processes that affect populations in complex landscapes. Oikos 65: 169-75.

Einum, S., Robertsen, G., Nislow, K.H., McKelvey, S., and Armstrong, J.D. 2011. The spatial scale of density-dependent growth and implications for dispersal from nests in juvenile Atlantic salmon. Oecologia (Berl.) 165(4): 959–969.

Esteve, M. 2005. Observations of spawning behaviour in Salmoninae: Salmo, Oncorhynchus and Salvelinus. Reviews in Fish Biology and Fisheries 15: 1–21.

Fielding, A.L., and Bell, J.F. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Envron. Conserv. 24: 38-49.

Fleming, I.A., Gross, M.R. 1994. Breeding competition in a Pacific salmon (Coho, *Oncorhynchus kisutch*): measures of natural and sexual selection. Evolution 48: 637-657.

Fleming, I.A. 1996. Reproductive strategies of Atlantic salmon: ecology and evolution. Reviews in Fish Biology and Fisheries 6: 379-416.

Flitcroft, R.L., Burnett, K.M., Reeves, G.H., and Ganio, L.M. 2012. Do network relationships matter? Comparing network and instream habitat variables to explain densities of juvenile coho salmon (*Oncorhynchus kisutch*) in mid-coastal Oregon, USA. Aquatic Conservation: Marine and Freshwater Ecosystems 22(3): 288-302.

Geist, D.R., and Dauble , D.D. 1998. Redd site selection and spawning habitat use by fall chinook salmon: the importance of geomorphic features in large rivers. Environmental Management 22(5): 655-669.

Good, T.P., Waples, R.S., and Adams, P. 2005. Updated status of federally listed ESUs of West Coast salmon and steelhead. NOAA Tech. Memo. NMFS-NWFSC-66, U.S. Dept. Commerce, Seattle, WA.

Groot, C., and Margolis, L. 1991. Pacific salmon life histories. *In* UBC Press, Vancouver, B.C.

Gurnell, A.M., Gregory, K.J., and Petts, G.E. 1995. The role of coarse woody debris in forest aquatic habitats: implications for management. Aquat. Conserv. 5:143-66.

Gurnell, A.M., Piegay, H., Swanson, F.J., and Gregory, S. V. 2002. Large wood and fluvial processes. Freshwater Biology. 47: 601–619.

Hendry, A.P., and Berg, O.K. 1999. Secondary sexual characters, energy use, senescence, and the cost of reproduction in sockeye salmon. Can. J. Zool. 77: 1663–1675.

Hendry, A.P., Berg, O.K., Quinn, T.P. 2001. Breeding location choice in salmon: causes (habitat, competition, body size, energy stores) and consequences (lifespan, energy stores). Oikos. 93: 407–418.

Hendry, A.P., Stearns, S.C., 2003. Evolution Illuminated: Salmon and their Relatives. Oxford University Press, Oxford, UK.

Hogan, D.L., Bird, S.A., and Hassan, M.A. 1998. Spatial and temporal evolution of small coastal gravel-bed streams: influence of forest management on channel morphology and fish habitats. *In*: Gravel –Bed Rivers in the Environment. Water Resources Publications, LLC. pp. 365-392.

Hosmer, D.W. and Lemishow, S. 2000. Applied logistic regression. John Wiley & Sons, New York.

Isaak, D.J., Thurow, R.F., Rieman, B.E., Dunham, J.B. 2007. Chinook salmon use of spawning patches: relative roles of habitat quality, size, and connectivity. Ecological Applications 17(2): 352-364.

Jensen, D.W., Steel, E.A., Fullerton, A.H., and Pess, G.R. 2009. Impact of fine sediment on egg-to-fry survival of Pacific salmon: a meta-analysis of published studies. Reviews in Fisheries Science 17: 348–359.

Johnson, C., Nielsen, S., Merrill, E., McDonald, T., and Boyce, M. 2006. Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. Journal of Wildlife Management 70: 347-357.

Kahler, T. H., Roni, P., and Quinn, T.P. 2001. Summer Movement and growth of juvenile anadromous salmonids in small western Washington streams. Can. J. Fish, Aquat. Sci. 58: 1947-1956.

Katz, S.L., Barnas, K., Hicks, R., Cowen, J., and Jenkinson, R. 2007. Freshwater habitat restoration actions in the Pacific Northwest: a decade's investment in habitat improvement. Restoration Ecology 15: 494-505.

Keating, K., and Cherry, S. 2004. Use and interpretation of logistic regression in habitat-selection studies. The Journal of Wildlife Management 68: 774-789.

Keller, E.A., and Swanson, F.J. 1979. Effects of large organic material on channel form and fluvial process. Earth Surface Processes 4: 361-380.

Kondolf, G.M. 2000. Assessing salmonid spawning habitat quality. Transactions of the American Fisheries Society 129: 262-281.

Kondolf, G.M., and Wolman, M.G. 1993. The sizes of salmonid spawning gravels. Water Resources Research 7: 2275-2285.

Laland, K.N., Sterelny, K., Odling-Smee, J., Hoppitt, W., and Uller, T. 2011. Cause and effect in biology revisited: is Mayr's proximate-ultimate dichotomy still useful? Science 334: 1512-1516.

Lichatowich, J. 1999. Salmon without rivers : a history of the Pacific salmon crisis. Island Press, Washington, DC.

MacKenzie, D.I. 2006. Modeling the probability of resource use: the effect of, and dealing with, detecting a species imperfectly. The Journal of Wildlife Management 70 (2): 367-374.

Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., and Erickson, W.P. 2002. Resource selection by animals, second edition. Kluwer Academic Publishers, Dordrecht, the Netherlands.

Manel, S., Williams, H.C., Ormerod, S.J. 2001. Evaluating presence/absence models in ecology: the need to account for prevalence. J. Appl. Ecol. 38: 921-931.

Mann, R.D., Caudill, C.C., Keefer, M.L., Roumasset, A.G., Schreck, C.B., and Kent, M.L. 2010. Migration behavior and spawning success of spring Chinook salmon in fall creek and the north fork middle fork Willamette River: relationships among fate, fish, condition, and environmental factors. Technical Report 2011-8-DRAFT. Idaho Cooperative Fish and Wildlife Research Unit. Moscow, ID.

McClure, M.M., Carlson, S.M., Beechie, T.J., Pess, G.R., Jorgensen, J.C., Sogard, S.M., and Sultan, S.E. 2008. Evolutionary consequences of habitat loss for Pacific anadromous salmonids. Evolutionary Applications 1: 300–318.

Merz, J.E. 2001. Association of fall-run Chinook salmon redds with woody debris in the lower Mokelumne River, California. California Fish and Game. 87(2): 51–60.

Montgomery, D.R., Buffington, J.M., Smith, R.D., Schmidt, K.M., Pess, G. 1995. Pool spacing in forest channels. Water Resources Research. 31: (4):1097-1105.

Moore, K.M.S., and Gregory, S.V. 1988. Summer habitat utilization and ecology of cutthroat trout fry (*Salmo clarki*) in Cascade Mountain streams. Can. J. Fish. Aquat. Sci. 45: 1921-1930.

Morris, D.W. 1989. Density-dependent habitat selection: testing the theory with fitness data. Evolutionary Ecology 3: 80-94.

Morris, D.W., Davidson, D.L., Krebs, C.J. 2000. Measuring the ghost of competition: insights from density-dependent habitat selection on the coexistence and dynamics of lemmings. Evol. Ecol. Res. 2: 41-67.

Mull, K.E., and Wilzbach, M.A. 2007. Selection of spawning sites by coho salmon in a northern California stream. North American Journal of Fisheries Management 27: 1343-1354.

Neville, H., Isaak, D.J., Thurow, R., Dunham, J., and Rieman, B. 2006. Microsatelite variation reveals weak genetic structure and retention of genetic variability in threatened Chinook salmon (*Oncorhynchs tschawytscha*) within a Snake River watershed. Conservation Genetics.

Nickelson, T.E., Solazzi, M.F., Johnson, S.L., and Rodgers, J.D. 1993. An approach to determining stream carrying capacity and limiting habitat for coho salmon (Oncorhynchus kisutch). *In* Proceedings of the Coho Workshop, 26–28 May 1992, Nanaimo, B.C. *Edited by* L. Berg and P.W. Delaney. Department of Fisheries and Oceans Canada, Vancouver, B.C. pp. 251-260.

Quinn, T.P. 1999. Variation in pacific salmon reproductive behaviour associated with species, sex and levels of competition. Behaviour 136: 179-204.

Quinn, T. 2004. Juvenile salmonids in streams. *In*. The behavior and ecology of pacific salmon & trout. University of Washington Press, Seattle, WA. pp. 188-189.

Ramsey, F.L., and Schafer, D.W. 2002. The statistical sleuth, a course in methods of data analysis, *Second Edition*. Duxbury Press, Belmont, CA.

Reeves, G.H., Benda, L.E., Burnett, K.M., Bisson, P.A., and Sedell, J.R. 1995. A disturbance-based approach to maintaining and restoring freshwater habitats of evolutionarily significant units of andromous salmonids in the Pacific Northwest. American Fisheries Society Symposium 17: 334-349.

Reiser, D.W., and Bjornn, T.C. 1991. Habitat requirements of anadromous salmonids. General Technical Report PNW-96. U.S. Forest Service, Portland, Oregon

Schluter, D., Price, T.D., and Rowe, L. 1991. Conflicting selection pressures and life history tradeoffs. Proceedings of the Royal Society of London B, Biological Sciences 246: 11-17.

Sear, D.A., and DeVries, P. 2008. Salmonid spawning habitat in rivers: physical controls, biological responses, and approaches to remediation. American Fisheries Society. Bethesda, USA.

Sedell, J.R., and Duval, S. 1985. Influence of forest and rangeland management on anadromous fish habitat in western North America: water transportation and storage of logs. USDA United States Forest Service General Technical Report GTR-PNW-186, Pacific Northwest Research Station, Portland, OR.

Sedell, J.R., and Luchessa, K.J. 1981. Using the historical record as an aid to salmonid habitat enhancement. *In* Acquisition and Utilization of Aquatic Habitat Inventory Information, Proceedings of Symposium 28-30 October 1981, Portland, OR. *Edited by* N.B. Arementrout. American Fisheries Society, Bethesda, MD, pp. 210-223.

Siepielski, A.M., DiBattista, J.D., Evans, J.A., and Carlson, S.M. 2011. Differences in the temporal dynamics of phenotypic selection among fitness components in the wild. Proceedings of the Royal Society B: Biological Sciences 277: 1572-1580.

Solazzi, M.F., Nickelson, T.E., Johnson, S.L., and Rodgers, J.D. 2000. Effects of increasing winter rearing habitat on abundance of salmonids in two coastal Oregon streams. Can. J. Fish. Aquat. Sci. 57: 906-914.

Stewart, G.B., Bayliss, H.R., Showler, D.A., Sutherland, W.J., and Pullin, A.S. 2009. Effectiveness of engineered in-stream structure mitigation measures to increase salmonid abundance: a systematic review. Ecological Applications 19(4): 931-941.

Swets, J.A. 1988. Measuring the accuracy of diagnostic systems. *Science* 240: 1285–1293.

Teichert, M.A.K., Foldvik, A., Forseth, T., Ugedal, O., Einum, S., Finstad, A.G., Hedger, R.D., Bellier, E. 2011. Effects of spawning distribution on juvenile Atlantic salmon (*Salmo salar*) density and growth. Can. J. Fish. Aquat. Sci. 68: 43–50.

Thomas, D.L., and Taylor, E.J. 2006. Study designs and tests for comparing resource use and availability II. Journal of Wildlife Management 70(2):324-336.

Thompson, W.L. and Lee, D.C. 2002. A two-stage information-theoretic approach to modeling landscape-level attributes and maximum recruitment of chinook salmon in the Columbia River basin. Natural Resource Modeling 15: 227-257.

Valone, T.J., and Templeton, J.J. 2002. Public information for the assessment of quality: a widespread social phenomenon. Philos. Trans. R. Soc. Lond. B Biol. Sc. 357: 1549–1557.

Van den Berghe, E. P., and Gross, M.R. 1989. Natural selection resulting from female breeding competition in a Pacific salmon (Coho: Oncorhynchus kisutch). Evolution 43: 125–140.

Wallace, J.B., Webster, J.R., and Meyer, J.L. 1995. Influence of log additions on physical and biotic characteristics of a mountain stream. Canadian Journal of Fisheries and Aquatic Sciences 52: 2120-2137.

White, S. M., and Rahel, F. J. 2008. Complementation of habitats for Bonneville cutthroat trout in watersheds influenced by beavers, livestock, and drought. Transactions of the American fisheries Society 137(3): 881-894.

Whiteway, S.L., Biron, P.M., Zimmerman, A., Venter, O., and Grant, J.W.A. 2010. Do in-stream restoration structures enhance salmonid abundance? A meta-analysis. Can. J. Fish. Aquat. Sci. 67(5): 831-841.

APPENDICES

Table A.1. Results from the logistic regression on the full model.

Parameter	Estimated Coefficient	S.E.	Odds ratio	95% C.I. for the odds ratio	
				Lower	Upper
Intercept	-15.22	2.132	--	--	--
Location	0.0003	0.0001	1.1592	1.1589	1.1595
Depth	0.4526	0.1204	1.572	1.250	2.010
Width/Depth	0.0707	0.036	1.073	1.000	1.151
Closest Redd	-0.0128	0.005	0.987	0.976	0.996
ELJ	-0.0532	0.024	0.948	0.903	0.992
Natural wood	-0.0561	0.025	0.945	0.896	0.989
Max depth	0.6050	0.095	1.936	1.621	2.352
Dist. to Pool Tail	-0.1490	0.035	.862	0.802	0.920

Table A.2. Density (redd/kilometer) of coho salmon breeding sites within the study reach (i.e. 4.5km). These density estimates included an additional 0.6 km of Little Wolf Creek in order to compare multiple years of data (J. McEnroe and S. Lightcap personal communication, Roseburg District Bureau of Land Management 2011).

Year	Number of redds/km
2006-07	12.0
2007-08	2.4
2008-09	8.3
2009-10	26.2
2010-11	22.8
2011-12	27.8

Table A.3. Raw data collected in Little Wolf Creek, Oregon as described in Methods.

Use	Stream Location	Depth	Width/ Depth	Closest Redd	ELJ	Natural Wood	Max Depth	Dist. to Pool Tail
1	1528.9	11	14.1	283.8	10	8	19	1.8
1	1572.9	9	22	0.1	0	32	20	15.6
1	1577.9	9	20.9	0.1	0	31	20	8.1
1	1761.7	13	12.2	19.2	13	6	16	1.9
1	1754.8	12	12.5	134.1	13	6	16	0
1	1797.4	13	11.1	14.8	10	3	16	3
1	1818	9	18.8	14.8	15	4	22	5
1	1904.8	11	11.1	19.6	0	8	17	2
1	2430.3	7	21.5	19.6	0	13	19	12
1	2547.3	9	16.5	1	0	17	18	2.4
1	2591.7	11	14.3	1	0	12	16	5
1	2715.9	12	15	11.3	0	29	17	8
1	2747.1	7	22.2	51.5	0	13	17	17.2
1	2921.6	11	14.3	16.4	0	4	18	2.6
1	2920.5	9	16.4	5	0	3	18	2.3
1	2947	9	13.1	5	0	2	17	4
1	2968.7	10	10.7	6.9	0	3	17	7.5
1	2976.9	10	13.6	6.9	0	3	17	3.7

1	2977.2	10	13.6	20.6	0	3	17	3.7
1	3023.5	9	12.6	20.6	0	2	13	2.3
1	3052.1	11	11.7	86.8	0	2	15	1.3
1	3052.1	11	11.7	117	0	2	15	1.3
1	3099.7	8	15.4	44.4	0	3	17	1.5
1	3100.6	11	12.1	40.4	0	3	17	2.5
1	3118	9	15.7	40.4	0	10	19	2.2
1	3174.9	8	20.9	18.6	0	6	16	4.2
1	3176.8	8	20.1	12.6	0	6	16	2.7
1	3177.2	10	17.5	12.6	0	6	16	0.8
1	3205.6	9	12.4	1.1	0	4	16	3.3
1	3227.6	7	17.7	1.1	0	7	14	16
1	3243.3	8	25.7	21.7	0	4	16	6
1	3246.2	8	21.4	5.5	0	4	16	2.2
1	3243.6	7	26.9	2.7	0	4	16	2.1
1	3243.6	8	23	0.3	0	4	16	9.5
1	3268.5	9	24.8	0.3	0	4	16	1.6
1	3356.4	10	27.4	28.6	0	12	15	1.5
1	3458.1	9	15.4	0	6	1	15	7
1	3482.7	9	12.9	0	6	0	15	1.7
1	3503.6	9	16.9	0.9	1	2	15	8.6
1	3551.7	10	12.8	0.9	13	4	17	0
1	3552.2	10	12.1	17.4	13	4	17	1.78

1	3567.6	9	12.3	1.9	0	3	13	6
1	3573.4	10	12.2	0.4	6	1	13	1.1
1	3735.8	7	16.3	0.4	0	8	18	6
1	3757.7	9	13.1	7.4	0	8	18	5.9
1	3846.6	9	28.7	7	20	1	14	8.6
1	3852.8	9	18.5	7	20	0	14	9
1	3901.1	10	12.5	15.7	20	9	15	4
1	3910.4	10	11.2	0.3	17	15	16	8.9
1	3918.1	7	17.5	0	16	14	16	7.9
1	3923.2	9	12.9	0	0	15	16	2.3
1	3926.4	9	13.7	2.6	0	15	16	3.2
1	4069.5	8	18.2	7.6	0	4	17	0.7
1	4069.8	8	18.2	14.7	0	4	17	0.7
1	4074.3	8	16.2	87.9	0	6	17	5.7
1	4230.3	8	15.6	24.6	0	5	12	14.7
1	4237.2	9	15.2	8.4	0	5	12	6.3
1	4240.6	8	15.7	8.4	0	4	14	3.5
1	4245.8	8	17.8	12.5	0	4	14	2.6
1	4320	7	30.6	0.5	0	5	15	10.4
1	4327.5	7	30.6	0.5	0	5	15	4.9
1	4339.9	7	21.4	5.8	0	5	15	4.1
1	4349.3	9	14.9	5.8	0	4	15	7.3
1	4862.3	10	11.9	25.3	0	4	16	13.9

1	4922.9	4	25.8	21.9	18	1	15	1.7
1	595.6	7	21.5	6	1	2	17	7.9
1	879.5	8	19.1	0.2	6	2	17	4.1
1	879.4	7	19.6	0.2	6	2	17	3
1	898.7	11	12.7	7.5	0	3	14	3.5
1	1189.4	10	14.9	9.3	20	2	15	2.4
1	1204.2	10	12.9	2.3	20	3	16	0
1	1277.9	10	7.8	2.3	0	5	16	2.4
1	1297.5	9	7.7	5.1	0	11	16	2.6
1	1348.7	9	10.9	3.2	0	7	17	15
1	1349.7	9	11.1	3.2	0	7	17	12.9
1	1361	9	14.8	0.3	0	4	15	2.5
1	1461	10	11.5	0.3	0	3	15	1.2
1	1512.5	9	14.2	4.5	10	0	17	0.8
1	1055.3	7	21.6	13.8	7	3	16	2.7
1	2632.1	8	21.2	6.9	0	9	16	6.3
1	2974.2	10	13.3	3.4	0	4	13	1.2
1	3191.2	11	9.3	0.3	0	6	17	18.3
1	3198.6	10	11.1	0.3	0	7	15	11.7
1	3253.8	8	21.7	4.9	0	3	17	9.4
1	3710.5	11	15.8	3.9	15	7	16	0.3
1	3774.4	9	17.9	3.9	13	4	17	1.4
1	3852.6	13	14.2	4.6	16	2	17	1.1

1	3860.3	15	10.5	4.6	25	2	17	6.4
1	3912.7	14	8.5	4.8	14	2	17	9.3
1	4331.4	12	19.1	25	0	8	16	4.5
1	4344.5	11	13.8	25	0	5	16	2.3
0	1526.1	11	13.3	2.8	7	12	7	8.3
0	1536.9	5	29.2	8	3	14	8	8
0	1624.8	6	23.3	46.9	0	9	32	2.2
0	1747.2	8	17.5	7.6	11	5	13	8.3
0	1805.1	12	11.7	7.7	10	4	13	15
0	1814.4	8	16.7	3.6	10	4	14	4
0	1842.2	11	12.5	24.2	4	6	14	3.7
0	1848.1	11	13.3	30.1	3	8	14	8
0	1902.8	9	16.5	2	0	6	11	2.4
0	1951.4	9	15.7	46.6	0	8	11	2.4
0	2050.9	7	21.5	15.9	0	9	12	2.3
0	2214.5	10	13.9	147.7	0	2	9	10.4
0	2296.8	10	14.7	133.5	0	0	13	2.4
0	2304.7	11	12.3	125.6	0	0	13	3.8
0	2313.6	10	13.7	116.7	0	0	13	4.9
0	2332.1	9	14.9	98.2	0	0	13	8.5
0	2398.8	9	15.4	31.5	0	1	12	3.9
0	2430.4	11	12.7	0.1	0	2	16	14.9
0	2533.4	10	14.6	13.9	0	17	13	13.2

0	2560.7	11	12.7	13.4	0	7	12	14.1
0	2594.3	10	14.7	1	0	11	11	5.8
0	2609	10	14	15.7	0	17	16	16
0	2635.2	10	13.7	3.1	0	11	17	2.9
0	2700.6	8	16.9	15.3	0	41	14	15
0	2766.1	8	17.1	15.1	0	59	17	3.6
0	2824.9	9	15.7	43.7	0	1	14	9.8
0	2859.8	8	18.7	60.7	0	2	15	0.9
0	2876.8	8	17.7	43.7	0	3	13	16.6
0	2913.1	6	22.2	7.4	0	2	14	13.4
0	2970	5	27.5	1.3	0	5	14	10.7
0	3009	11	13.3	14.5	0	2	13	16.3
0	3048.1	8	17.7	4	0	2	15	4.7
0	3097.2	8	17.1	2.5	0	2	14	2.9
0	3182.2	10	13.6	5	0	8	15	4
0	3196	10	13.6	2.6	0	6	15	12.1
0	3216.3	12	11.7	10.7	0	6	13	7.5
0	3242.3	6	23.3	1	0	6	15	3.1
0	3234.1	8	17.3	5.1	0	6	14	11.4
0	3272.1	7	20.9	3.6	0	9	16	5.4
0	3337.9	9	15.6	18.5	0	6	15	18.6
0	3337.9	9	15.6	18.5	0	12	15	15.8
0	3365.9	10	13.7	9.5	0	12	13	7.2

0	3426.8	7	18.9	31.3	0	3	15	17.6
0	3444.9	11	12.7	13.2	2	4	14	13.1
0	3448.1	9	14.9	10	2	4	14	11
0	3403.8	11	13.6	47.4	2	3	12	7
0	3503.4	11	13.8	0.2	1	4	12	5.4
0	3516.4	10	10.4	12.8	12	10	15	15.7
0	3562.3	10	10.3	5.3	0	3	14	6.3
0	3584.6	11	10.4	11.2	14	1	14	9.3
0	3685	9	15.4	25.5	13	8	15	6.5
0	3713.4	10	12.6	2.9	12	13	14	7.4
0	3748.8	9	12.4	8	0	12	18	4.7
0	3785.6	11	23	4	11	17	14	9.5
0	3787.6	9	27.3	3.2	11	17	14	6.6
0	3841.1	10	22.9	5.5	27	4	15	3.5
0	3860.6	9	14.7	0.3	30	3	16	2
0	3865.6	8	11.5	1.6	36	3	15	4.8
0	3900.5	10	11.4	0.6	14	11	13	5
0	3922.1	10	11.7	1.1	2	11	15	1.4
0	3949.7	11	10.3	23.3	0	0	16	6.8
0	4059	11	10.6	10.5	0	12	15	3.8
0	4065.4	7	19.3	4.1	0	11	15	9.8
0	4004	10	12	65.5	0	38	15	12.9
0	4187.2	9	11.4	9	0	9	16	11

0	4213.6	7	22.5	0.5	0	10	14	3.1
0	4225.7	7	16.9	4.6	0	6	14	12.1
0	4257.5	10	11	11.8	0	4	13	11.8
0	4319.5	6	30.9	0.5	0	8	14	11.1
0	4320.5	4	50.3	0.5	0	6	14	9.9
0	4329	8	28.4	1.5	0	6	14	0.2
0	4349	8	17.6	0.3	0	6	14	12.1
0	4375	9	10.7	25.7	9	1	12	5.5
0	4411.7	7	16.1	62.4	0	1	15	7.4
0	4457.1	8	15.3	107.8	21	0	14	7.9
0	4470	8	13.3	120.7	16	1	10	3.7
0	4501.7	7	15.8	152.4	0	1	16	16.7
0	4623.3	7	16.4	239	0	0	14	6.4
0	4655.9	11	9.9	206.4	6	0	13	1.1
0	4666	9	10.1	196.3	29	0	13	11.8
0	4830.5	13	9	31.8	13	11	15	8.1
0	4844.1	11	13	18.2	3	12	12	6
0	4867.3	10	10.9	5	0	3	15	9.8
0	4875.2	6	20.8	12.9	2	1	15	1.3
0	4896.6	11	8.3	26.3	11	1	15	4.5
0	639.4	7	23.1	37.7	0	3	17	1.5
0	834.3	8	18.1	45.1	7	4	15	7.1
0	833.7	9	15.9	45.7	7	4	15	4.6

0	870.3	9	12.6	9.1	8	3	16	9.5
0	883.5	9	15.7	4	5	4	16	2.8
0	885.3	6	23.6	5.8	1	5	15	5.1
0	907.5	8	17	8.8	0	5	15	5.1
0	938.3	9	14.8	39.6	0	4	12	19.2
0	962.5	10	14.8	63.8	5	4	17	4.5
0	963.1	9	15.4	64.4	5	4	17	4.5
0	1172.4	7	22.2	17	5	2	12	1.7
0	1177.6	8	16.3	11.8	12	2	12	5
0	1200	6	18.7	4.2	12	1	15	5.7
0	1223.9	8	14.6	0	0	8	14	3.2
0	1281.4	9	8	3.5	0	16	14	2.7
0	1273.1	8	6.5	4.8	0	16	14	4.8
0	1304.3	7	5.7	6.8	0	31	14	3
0	1322.5	8	7.5	25	0	23	15	7.9
0	1375.8	7	12.9	8.7	0	3	13	12.9
0	1451.9	9	6.2	9.1	0	3	14	11.7
0	1495.3	10	11.9	17.2	2	1	15	16.1
0	1505.9	8	15.1	6.6	9	1	15	6.2
0	576.2	11	14.7	19.4	29	1	20	4.1
0	578.2	8	18.9	17.4	29	1	20	6.5
0	762.2	9	19.8	117.2	18	10	11	6.5
0	788.6	6	22.2	90.8	0	19	11	18.7

0	930.1	8	15.9	31.4	0	4	11	10.9
0	1304.3	10	4.4	6.8	0	38	14	2.8
0	1309.3	7	5.7	11.8	0	37	14	1.6
0	1376.8	9	12.3	9.7	0	2	14	5.4
0	1471.9	8	12.1	10.9	0	4	14	10.5
0	1515.9	9	13.2	3.4	9	0	16	6.4
0	1542.9	9	15	14	1	48	15	13.9
0	1770.4	7	10.7	8.7	9	2	15	15.2
0	1889.7	6	20.3	15.1	0	11	12	15.1
0	1918.5	5	22.4	13.7	0	16	11	14.5
0	2298.8	10	11.1	131.5	0	2	13	11.2
0	2319.6	6	21.7	110.7	0	0	11	4.6
0	2384.8	8	14.6	45.5	0	2	14	9.6
0	2478.4	7	19.4	48.1	0	3	18	2.9
0	2478.4	12	11.7	48.1	0	3	18	3.7
0	2702.7	9	21.1	13.2	0	40	16	2.8
0	2906.1	9	15.1	14.4	0	3	14	6.5
0	2918.1	7	16.5	2.4	0	4	14	18.8
0	3011.6	4	36	11.9	0	9	15	5.6
0	3146	8	15.9	21	0	20	13	6.6
0	3180.2	9	14.1	3	0	8	15	4.5
0	3428.8	8	13.8	29.3	0	4	15	19.3
0	3524.7	6	21.7	21.1	21	5	16	13.5

0	3585.6	8	15.8	12.2	18	2	15	11.5
0	3753.8	10	10.5	3.9	10	7	14	9.7
0	3755.8	12	9.3	1.9	8	6	14	11
0	3811.1	9	5.9	20.3	3	12	14	2.9
0	3941.7	11	13.2	15.3	0	7	17	17.6
0	3971.9	9	13.8	45.5	0	0	13	1
0	4260.1	10	11.9	14.4	0	2	14	15.3
0	4328.5	6	22.5	1	0	6	13	4.8
0	4420.7	7	19.4	71.4	8	2	12	3
0	4482.5	9	13.1	133.2	8	2	10	6.6
0	4492.5	8	15.1	143.2	0	2	10	3.5
0	4654.8	7	18.3	207.5	6	0	11	1.1
0	4879.2	9	13.2	16.9	4	3	14	1.28
0	4893.2	8	11.4	29.7	9	3	14	4.9
0	586.2	7	22.5	9.4	23	1	13	16.9
0	796.6	9	18.8	82.8	0	13	12	9.7
0	818.3	8	24	61.1	7	5	12	10.9
0	874.3	8	13.4	5.1	6	4	13	6.3
0	998.9	8	15.5	55.5	10	0	11	10.3
0	1281.4	10	7.7	3.5	0	19	12	2.6
0	1309.3	8	4.8	11.8	0	34	12	3
0	1320.4	9	7.5	22.9	0	24	15	9.3
0	1505.9	9	12.9	6.6	7	0	14	7.6

0	1525.9	9	15.9	3	7	4	13	3.7
0	1571.9	9	19.9	1	0	18	14	15.5
0	1734.9	7	12.4	19.9	8	3	12	4.5
0	1822.4	7	18.5	4.4	14	3	16	2.9
0	1927.5	7	19.4	22.7	0	9	13	6.7
0	2067.8	8	14.9	34.3	0	10	12	4.4
0	2367.4	7	18.5	62.9	0	3	10	7.1
0	2392.8	8	15.7	37.5	0	1	12	2
0	2472.4	9	14.5	42.1	0	3	17	3.3
0	2508	10	13.4	39.3	0	11	14	2.5
0	2611.3	9	14.6	18	0	13	14	12.4
0	2714.7	7	29	1.2	0	16	15	8.3
0	2763.1	8	20.2	16	0	32	11	5.5
0	2871.8	6	14.7	48.7	0	3	14	5.8
0	2921.1	9	11.5	0.5	0	2	15	19.9
0	2961	6	12.5	7.7	0	2	12	8.9
0	3048.1	8	16.4	4	0	3	12	4
0	3102.2	8	17.8	1.6	0	4	13	2.6
0	3150	8	11.2	17	0	10	13	1.8
0	3216.3	13	10.6	10.7	0	5	13	7.4
0	3336.9	7	25.7	19.5	0	9	15	17
0	3503.8	8	14.8	0.2	0	2	12	5.2
0	3575.6	5	22.5	2.2	8	2	13	1.1

0	3692.4	9	17	18.1	15	4	12	10
0	3867.6	9	5.9	0.4	3	11	14	17.5
0	3867.6	9	9.2	0.4	8	3	12	7.4
0	3886.5	10	12.9	14.6	15	2	12	6.4
0	3942.7	11	13.7	16.3	0	8	13	17.6
0	4060.4	7	15.9	9.1	0	11	15	5.1
0	4115.2	7	20.7	40.9	0	17	12	3.6
0	4198.2	9	12.9	15.9	0	9	14	15.3
0	4220.7	7	14.6	4.2	0	4	13	7.9
0	4254.1	7	17.2	8.4	0	3	12	10.9
0	4312.5	9	17.6	5.9	0	4	12	13.1
0	4409.7	8	12.5	60.4	0	0	12	9.5
0	4681.2	8	14.3	181.1	35	0	10	5.5
0	4795.6	9	15.4	66.7	13	0	13	2.8
0	4865.2	10	11.2	2.9	0	4	15	11.1
0	4928.4	9	14.6	5.5	14	1	13	3.7
0	803.6	5	37.9	75.8	2	6	14	1.9
0	1138.8	10	17.5	50.6	13	1	13	18.1
0	1177.6	8	18.3	11.8	12	1	11	6.7
0	1219.7	7	25.4	4.2	0	5	12	5.8
0	1280.1	8	9.9	2.2	0	14	12	3.1
0	1317.5	9	9	20	0	13	16	10.5
0	1359.7	6	16.4	1.3	0	1	13	3.8

0	1456.9	7	11.5	4.1	0	0	15	8
0	1478.3	5	18.7	17.3	0	2	15	13.8
0	1517.1	9	13.6	4.6	8	1	14	11.6
0	1568.1	8	18.3	4.8	0	18	16	16.9
0	1582.9	5	30.4	5	0	8	14	8.7
0	1735	7	10.7	19.8	0	8	15	4.2
0	1758.2	8	16.3	3.4	10	1	13	1.4
0	1793.1	6	27.2	4.3	4	2	13	18.5
0	1877.1	8	21.1	27.7	0	8	13	7.7
0	1958.4	11	13.2	53.6	0	7	14	5.8
0	2052.9	7	14.4	13.9	0	12	11	3.5
0	2097	7	17.8	30.2	0	3	15	13.1
0	2214.7	8	12	147.9	0	0	12	3.1
0	2304.7	6	18.4	125.6	0	0	13	5.3
0	2385.5	8	15.8	44.8	0	3	12	9.7
0	2404.8	6	18.3	25.5	0	3	12	10.7
0	2438.4	6	25.5	8.1	0	3	19	9.9
0	2482.9	10	15.1	52.6	0	3	18	4.9
0	2588.3	8	14.6	3.4	0	7	12	8.7
0	2614	10	10.2	18.1	0	8	14	16.6
0	2692.6	10	14.9	23.3	0	16	13	5.2
0	2833.9	8	14.8	52.7	0	1	11	2.5
0	2930.8	9	10.4	9.2	0	1	14	16.3

0	2973.6	6	18.2	0.6	0	3	13	7.7
0	3108	7	22.7	7.4	0	5	15	9.8
0	3168.1	8	20.7	1.1	0	14	14	1.83
0	3219.3	11	10.5	8.3	0	6	13	10.5
0	3352.9	9	23.2	3.5	0	8	12	2.8
0	3404.8	7	18.9	48.4	0	2	14	5.2
0	3555.3	7	14.5	3.1	12	2	19	19
0	3684	6	25.3	26.5	12	4	13	2.2
0	3784.6	10	17.7	3	11	9	15	2.3
0	3875.6	8	15.1	8.4	18	1	11	1.5
0	3921.1	8	15.3	2.1	2	6	14	3.5
0	4093.6	8	16.6	19.3	0	16	13	0.9
0	4177.8	8	15.1	0.4	0	13	15	2.9
0	4257.5	8	13.7	11.8	0	4	12	12.3
0	4338.5	8	18	1.4	0	5	15	11.9
0	4361	8	17	11.7	7	3	13	6.3
0	4383.5	6	22.4	34.2	10	0	13	12.2
0	4519.7	7	19.4	170.4	0	2	15	3
0	4831.5	10	12.9	30.8	15	13	15	5.7
0	4843.3	11	13.5	19	5	12	12	7.2
0	4900.6	9	13.3	22.3	11	1	15	20
0	4942.8	7	19.7	1	14	5	13	2.6
0	599.6	7	21.4	0	1	2	15	7.6

0	768.2	10	21.8	111.2	16	14	12	15.9
0	819.6	6	25.6	59.8	6	6	14	2.9
0	913.5	9	13.5	14.8	0	5	13	2.6
0	1196	7	21.2	6.6	12	0	15	10.4
0	1345.7	6	17.2	3	0	9	15	16.3
0	1540.9	10	14.4	12	2	21	15	10.6
0	1599.9	12	12.2	22	0	9	16	14.8
0	1735	8	11.7	19.8	8	1	13	4.7
0	1822.2	7	23	4.2	15	3	16	1.1
0	1951.4	8	17.1	46.6	0	6	16	1.8
0	2029.5	5	25.7	37.3	0	12	11	3.4
0	2090	11	15	23.2	0	0	12	4.5
0	2345.4	9	16	84.9	0	2	13	19.1
0	2393.8	8	15.2	36.5	0	1	12	5.3
0	2700.7	10	21.3	15.2	0	31	14	3.5
0	2865.8	8	14.7	54.7	0	3	12	10.1
0	2916.8	7	14.9	3.7	0	1	15	18.7
0	3184	10	9.8	6.8	0	7	15	5.4
0	3259.1	7	24	3.6	0	6	16	15.6
0	3447.9	8	18.5	10.2	2	3	13	14.6
0	3559.3	10	10.2	7.1	6	4	12	12.9
0	3681	9	16.4	29.5	15	6	14	6.2
0	3758.8	14	8	1.1	6	3	15	17.9

0	3794.6	7	35.8	3.8	17	8	15	3.1
0	3867.6	10	12.5	0.4	13	2	14	5.8
0	4259.5	8	15.2	13.8	0	2	13	13.8
0	4313.5	9	19.1	4.9	0	4	12	12.3
0	4363	7	18	13.7	8	1	12	2.8
0	4879.2	6	19.3	16.9	3	0	15	4.4